



Hymenobacter jejuensis sp. nov., a UV radiation-tolerant bacterium isolated from Jeju Island

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Abstract A novel Gram-stain negative, aerobic, rod-shaped, non-motile and pink-coloured bacterium, designated strain 17J68-5^T, was isolated from soil in Jeju Island, Korea. The strain was found to grow at 18–37 °C (optimum 25 °C) in R2A medium at pH (6.0 to 7.5; optimum 6.5) in the presence of 0% (w/v) NaCl. Phylogenetic analysis based on 16S rRNA gene sequences indicated that strain 17J68-5^T forms a distinct lineage within the family *Hymenobacteraceae* and is closely related to *Hymenobacter daecheongensis* DSM 21074^T (94.9% 16S rRNA gene sequence similarity), *Hymenobacter rutilus* K2-33028^T (94.6%) and *Hymenobacter tibetensis* XTM003^T (94.3%). The draft genome sequence of strain 17J68-5^T is 5.1 Mb size. The calculated average nucleotide identity and the digital DNA–DNA hybridization between strain 17J68-5^T and closely related type strains were 81.3 to 84.1 % and 25.5 to 28.1%. The major cellular fatty acids ($\geq 10\%$) of the strain 17J68-5^T were identified

as summed feature 3 (C_{16:1} ω6c/C_{16:1} ω7c; 21.2%), iso-C_{15:0} (19.1%), summed feature 4 (C_{17:1} iso I/C_{17:1} anteiso B; 17.9%) and C_{16:1} ω5c (13.1%). The predominant respiratory quinones were found to be menaquinone 7 and 6 (MK-7 and MK-6). The major polar lipid was found to be phosphatidylethanolamine. The genomic DNA G + C content based on the whole genome sequence is 59.6 mol %. The phenotypic, chemotaxonomic and genotypic properties clearly indicated that isolate 17J68-5^T represents a novel species within the genus *Hymenobacter*, for which the name *Hymenobacter jejuensis* sp. nov. is proposed. The type strain of *Hymenobacter jejuensis* is 17J68-5^T (= KCTC 62224^T = JCM 33182^T).

Keywords *Hymenobacteraceae* · *Hymenobacter* · UV radiation · Novel strain

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Introduction

UV radiation has a major impact on the environment and damages living organisms. UV radiation is readily absorbed by DNA and leads to mutations (D’Orazio et al. 2013). Some UV radiation can trigger the formation of reactive oxygen species and causes cell or tissue damage in the form of oxidation of DNA, proteins and lipids (Choi et al. 2018; Jang et al. 2017). Nevertheless, living cells have developed the ability to self-repair their own DNA damage (Yu and Lee 2017).

Overall, the level of ionizing radiation resistance is related to genetic and physiological characteristics of organisms. Systems such as the enzymatic machinery of DNA repair, perform important roles in cell recovery after exposure to ionizing radiation (Krisiko and Radman 2013). Studies on microbial diversity and isolation of novel radiation resistant bacteria are widely reported, as well as the complete genome sequences of UV resistant bacteria such as *Hymenobacter sedentarius*, *Hymenobacter* spp., *Methylobacterium* spp., *Microvirga* spp., *Nibrubacter radioresistens* and *Spirosoma pulveris*, (Kang and Srinivasan 2018; Kim et al. 2017a, b; Sathiyaraj et al. 2018a, b; Srinivasan et al. 2017), in order describe their role on ionizing radiation resistance.

The genus *Hymenobacter* was first described by Hirsch et al. (1998) and belongs to the family *Hymenobacteraceae*. At the time of writing, the genus comprises 67 species (<http://www.bacterio.net/hymenobacter.html>). *Hymenobacter* species have been found to survive in extreme conditions such as sandstone sediments (*Hymenobacter qilianensis*; Han et al. 2014), freshwater (*Hymenobacter aquatilis*; Kang et al. 2018), desiccation (*Hymenobacter deserti*; Zhang et al. 2009), radiation (*Hymenobacter sedentarius*; Kim et al. 2017a), heavy metals (*Hymenobacter flocculans*; Chung et al. 2010) and glacial ice (*Hymenobacter antarcticus*; Klassen and Foght 2011). In general, members of *Hymenobacter* are rod-shaped, Gram-negative, red to pink-coloured and aerobic with menaquinone-7 (MK7) as their major isoprenoid quinone and phosphatidylethanolamine (PE) as the major polar lipid. Moreover, according to previous iso- $C_{15:0}$, anteiso- $C_{15:0}$, $C_{16:1}$ $\omega 5c$, summed feature 3 ($C_{16:1}$ $\omega 7c$ and/or $C_{16:1}$ $\omega 6c$) and summed feature 4 (iso- $C_{17:1}$ I and/or anteiso- $C_{17:1}$ B) as the major fatty acids (Zhu et al. 2017). In this study we isolated a novel UV radiation tolerant strain, 17J68-5^T, from a soil sample collected on Jeju Island, South Korea and the 16S rRNA sequence similarity determined that strain 17J68-5^T belongs to the genus *Hymenobacter*. The strain was subjected to a polyphasic analysis was conducted to determine the precise taxonomic position of strain 17J68-5^T.

Materials and methods

Strain isolation and maintenance

Strain 17J68-5^T was isolated from a soil sample collected in Jeju Island (33.450049°N, 126.321168°E), South Korea. 0.2 g soil sample was added to 0.9 mL of sterile water (10^{-1} dilution) and 100 μ L of the suspension were spread on the surface of R2A agar plates at 28 °C and incubated for 1 week. An isolate which formed red to pink coloured colonies was isolated and purified using R2A medium (Difco). The plates were incubated at 25 °C for 3 days. The colonies were maintained as glycerol stocks (20%, w/v) in R2A medium and the ampoules were stored at – 80 °C. The purified colonies were identified using partial 16S rRNA gene sequences using the EzTaxon server (<https://www.ezbiocloud.net/>) (Yoon et al. 2017).

The reference strain *Hymenobacter daecheongensis* KCTC 22258^T, obtained from Korean Collection of Type cultures and was cultured in R2A medium at 25 °C for 3 days and included for experiments for comparative purposes. All the strains were grown in the same conditions for the experiments.

Phenotypic characteristics

The morphological characteristics of strain 17J68-5^T were examined using cells grown on R2A agar for 2–3 days at 25 °C by transmission electron microscopy (JEOL, JEM1010). Colony characteristics were observed after incubation of the bacterial cells at 25 °C for 3 days on R2A agar (Difco). Growth on different bacteriological culture media was evaluated by using R2A agar (Difco), nutrient agar (NA; Difco), tryptone soya agar (TSA; Difco) and Luria–Bertani agar (LBA; Difco). Gram-staining was performed using a commercial kit, following the manufacturer's instruction (bioMérieux). A motility test was performed in SIM medium (Oxoid) and R2A medium supplemented with 0.4% agar. Oxidase and catalase activity were examined by the addition of 1% (w/v) tetramethyl-p-phenylene diamine and 3% (w/v) H₂O₂ solution, respectively (Cappuccino and Sherman 2002). Growth at different temperatures (4, 10, 15, 18, 20, 25, 30, 37, 42 and 45 °C) was assessed on R2A agar for 3 days at 25 °C. NaCl tolerance of cells was tested up to 2% salt concentration. Growth pH (4 to 10,

0.5 pH intervals) and different salt concentrations was assessed on R2A medium for 3 days and at 25 °C. For the pH test, the R2A medium was adjusted to pH 4.0–11.0 (at intervals of 0.5 pH units) prior to autoclaving using 0.1 M citrate/NaH₂PO₄ buffer (for pH range 4.0–5.5), 0.1 M phosphate buffer (for pH range 6–7.5), 0.2 M Tris buffer (for pH range 8–10) and 5 M NaOH (for pH range 10.5–11.0). API 20NE, 32GN and API ZYM tests were performed according to the instructions of the manufacturer (bioMérieux).

Genome sequencing and phylogenetic analysis

The genomic DNA was extracted using a commercial genomic DNA extraction kit (Solgent, Korea). The draft genome sequence of strain 17J68-5^T was sequenced using a PacBio RS II platform at DNA Link (www.dnalink.com), Korea. The assembly of the genome sequence was done using a hierarchical genome assembly process (SMRT Analysis HGAP.3 Version 2.3) including consensus polishing with Quiver (Chin et al. 2013). The genome sequence has been deposited in GenBank (www.ncbi.nlm.nih.gov/) database and annotated using the National Center for Biotechnology Information Prokaryotic Genome Annotation Pipeline (PGAP) (Tatusova et al. 2016). To estimate the overall similarity among compared genomes, average nucleotide identity (ANI) and digital DNA–DNA hybridization (dDDH) was used. ANI values were calculated using the Orthologous Average Nucleotide Identity Tool version 0.98 (Lee et al. 2015) and dDDH using the Genome-to Genome Distance Calculator (GGDC) web server (<http://ggdc.dsmz.de>).

The 16S rRNA genes of strain 17J68-5^T were amplified using the 27F and 1492R universal bacterial primer set (Weisburg et al. 1991), then sequenced by Macrogen (Korea) using the 337F, 518R, 785F, and 926R universal bacterial primer sets (Kim et al. 2005). The 16S rRNA sequences of related taxa were obtained from EzBioCloud and edited with the EzEditor2 program (Jeon et al. 2013). Multiple alignments were performed with the CLUSTAL X program (Thompson et al. 1997). The gaps at 5' and 3' ends was cut using Bioedit (Hall 1999). Phylogenetic trees were constructed using the MEGA7 program (Tamura et al. 2016) using the neighbour-joining (Saitou and Nei 1987), maximum-likelihood (Felsenstein 1981) and maximum-parsimony (Fitch 1971) methods. Evolutionary distances were

calculated with the Kimura two-parameter model (Kimura 1983). The bootstrap values were calculated based on 1000 replicates (Felsenstein 1985). The GenBank accession number for the 16S rRNA gene sequence of strain 17J68-5^T is MH588267.

Chemotaxonomic studies

To identify fatty acids, cells were incubated on R2A for 3 days at 25 °C. Fatty acids were then purified by saponification, methylation and extraction procedures, as described previously (Sasser 1990). The fatty acid methyl esters were identified using the Sherlock Microbial Identification System V6.01 (MIS, database TSBA6, MIDI Inc., Newark, DE, USA). Polar lipids were extracted (Minnikin et al. 1984), separated using two-dimensional thin layer chromatography and the different spots were observed by spraying with the appropriate detection reagents (Komagata and Suzuki 1987). Respiratory quinones were extracted with Sep-Pak Vac cartridges (Waters, USA) and menaquinones were analysed by high performance lipid chromatography based on previous methods (Hiraishi et al. 1996).

UV radiation survival test

For identification of radiation resistant bacteria, pure cultures of isolates were used. The UV resistance survival test was studied according to Im et al. (2013) and Selvam et al. (2013). Cells were irradiated with a UVC cross-linker (UVP, CX-2000, USA) at 254 nm and was used with different dose adjustments. After being exposed to UV radiation, the survival rates of strain 17J68-5^T, *Deinococcus radiodurans* R1^T (DSM 20539^T), positive control) and *Escherichia coli* K-12 (KCTC 1116^T, negative control) were measured using cells in the early stationary phase ($\approx 10^9$ c.f.u. ml⁻¹) on R2A agar medium (Difco). The numbers of colony-forming units (CFU) of the strains were counted and the survival rate was calculated based on CFU values.

Results and discussion

Phenotypic characterisation

The images from transmission electron microscopy revealed the morphology of strain 17J68-5^T to be short

Table 1 Differential characteristics of strain 17J68-5^T and closely related species of *Hymenobacter*. Strains: 1, 17J68-5^T; 2, *H. daecheongensis* KCTC 22258^T; 3, *H. rutilus* K2-33028^T; 4, *H. tibetensis*

Characteristic	1	2	3	4
Cell shape	Rod shape	Rod shape	Rod shape	Rod shape
Size (µm long)	0.8–1.2	2.0–5.0	1.6–2.4	0.3–0.4
Size (µm wide)	0.6–0.8	0.6–1.0	0.8–1.0	0.8–1.2
Colony color	Pink	Pink	Brick red	Brick red
Optimum growth temperature (°C)	30	30	28	25
Temperature range (°C)	18–37	4.0–30	4.0–37	4.0–30
Optimum pH	6.5	7.5	7.0	7.0
pH range	6.0–7.5	5.0–10	6.0–8.0	5.0–10.0
Optimum NaCl (%)	0	0	0	1
Enzyme activity				
<i>N</i> -Acetyl-β-glucosaminidase	+	–	–	+
Cystine arylamidase	+	–	+	w
Esterase (C4)	w	+	+	+
α-Galactosidase	+	–	–	–
β-Galactosidase (ONPG)	+	–	–	+
β-Galactosidase (PNPG)	+	–	ND	ND
α-Glucosidase (starch hydrolysis)	+	–	–	–
β-Glucosidase (Esculin hydrolysis)	+	–	w	W
β-Glucosidase	+	–	–	+
β-Glucuronidase	w	–	w	–
Lipase (C14)	w	–	ND	–
α-Mannosidase	w	–	–	–
Naphthol-AS-BI-phosphohydrolase	+	–	W	+
Trypsin	+	–	–	–
Valine arylamidase	+	–	ND	ND
Assimilation				
L-Arabinose	–	–	+	+
D-Mannitol	–	+	ND	–
D-Sorbitol	–	+	ND	–
<i>N</i> -Acetyl-β-glucosamine	–	+	–	–
Salicin	–	+	ND	ND
Glycogen	–	+	ND	ND
Quinone	MK-6,7	MK-7	MK-7	MK-7
G + C content (%)	59.6	63.1	64.4	55.8

+, Positive; –, negative; w, weak and ND, not determined. Data for reference strains (except *H. daecheongensis*, this study) are from Kim et al. (2017a, b, c, d) and Dai et al. (2009)

rod shaped with a size range of 0.6–0.8 × 0.8 µm (Supplementary Fig. S1). The colonies of strain 17J68-5^T are convex, smooth, circular and pink-coloured after 3 days growth at 25 °C on R2A agar medium. Cells are Gram-negative and the strain can grow between 18 and 37 °C with pH range 6.0 and 7.5. No growth was observed in the presence of NaCl (up to 2%) in R2A broth. Growth was observed on NA and R2A but not on TSA agar. The other physiological characteristics of the strain 17J68-5^T and related type

strains are shown in Table 1. In API 20NE tests, esculin hydrolysis, gelatin hydrolysis, β-galactosidase are positive, but negative reactions were observed for nitrate reduction, indole production, glucose fermentation, arginine dihydrolase, urease, D-glucose, L-arabinose, D-mannose, D-mannitol, *N*-acetyl-D-glucosamine, D-maltose, gluconate, caprate, adipate, L-malate, citrate and phenyl acetate. In API ZYM tests, strain 17J68-5^T was found to produce alkaline phosphatase, esterase (C8), leucine arylamidase, valine

arylamidase, cystine arylamidase, trypsin, acid phosphatase, naphthol-AS-BI-phosphohydrolase, α -galactosidase, β -galactosidase, starch hydrolysis, β -glucosidase, *N*-acetyl- β -glucosaminidase, esterase (C4) (weak, w), lipase (C14) (w), β -glucuronidase (w) and α -mannosidase (w). Does not produce α -chymotrypsin and α -fucosidase.

Genome sequence and phylogenetic analysis

The draft genome sequence of strain 17J68-5^T is 5.1 Mb and consists of 5996 total genes, among them 5746 coding genes (CDS), 123 RNA and 127 pseudogenes with G + C content of 59.6% (Table S1). The draft genome sequence of the strain 17J68-5^T has been deposited in GenBank under the accession number CP040896. The PCR amplification and sequencing of the 16S rRNA gene was performed and the amplified product size was 1451 bp. The 16S rRNA gene sequences from PCR and the draft genome sequence were identical. Multiple sequence alignment was carried out with 16S rRNA sequences of 30 type strains in the genus *Hymenobacter*. The phylogenetic analysis based on 16S rRNA gene sequences indicated that strain 17J68-5^T is closely related to *H. daecheongensis* DSM 21074^T (94.9% 16S rRNA gene sequence similarity), *Hymenobacter rutilus* K2-33028^T (94.6%) and *Hymenobacter tibetensis* XTM003^T (94.3%). The sequence similarities between strain 17J68-5^T and other *Hymenobacter* species were less than 94%. The phylogenetic analysis presented by a neighbor-joining tree (Fig. 1), together with the topologies generated by the maximum likelihood and maximum parsimony algorithms (Supplementary Figs. S2 and S3), showed the relationship of strain 17J68-5^T with other *Hymenobacter* species. A threshold of < 97% similarity in 16S rRNA gene sequence was proposed for bacterial species delineation by Stackebrandt and Goebel (1994). Later, the species delineation threshold was increased to < 98.7% (Kim et al. 2014). On the basis of threshold values, the above data indicate that strain 17J68-5^T represents a novel species of the genus *Hymenobacter*. For further confirmation, the whole genome sequence of strain 17J68-5^T was analysed for ANI and dDDH with related available genomes of *Hymenobacter* species. The calculated orthoANI values between strain 17J68-5^T with closely related *H. daecheongensis* Dae14^T, *H. norwichensis* DSM 15439^T, *H. perfusus* A1-12^T and *H. swuensis*

DY53^T were 75.4, 73.8, 73.8 and 73.7%, respectively (Fig. S4). The dDDH values between strain 17J68-5^T and *H. daecheongensis* Dae14^T, *H. norwichensis* DSM 15439^T, *H. perfusus* A1-12^T and *H. swuensis* DY53^T were 20.4, 19.5, 19.9 and 20.0% (Table S2). The information held in genome sequences provides objective and reliable methods for the taxonomy of prokaryotes (Chun et al. 2010). The ANI and dDDH values between the strain 17J68-5^T and related taxa are below the cut-off values of ≥ 95 –96% for ANI (Richter and Rosselló-Móra, 2009) and ≥ 70 % for dDDH (Meier-Kolthoff et al. 2013) used to define bacterial species.

Chemotaxonomic characteristics

The major fatty acids of strain 17J68-5^T were identified as summed feature 3 (C_{16:1} ω6c/C_{16:1} ω7c) (21.2%), C_{15:0} iso (19.1%), summed feature 4 (C_{17:1} iso I/C_{17:1} anteiso B) (17.9%) and C_{16:1} ω5c (13.1%). The fatty acid profiles of strain 17J68-5^T compared with related strains are shown in Table 2. The fatty acid profile of strain 17J68-5^T is similar to those of phylogenetically related strains. Strain 17J68-5^T was found to contain major amount of PE, two unidentified aminophospholipids and one phospholipid and minor amounts of two unidentified lipids (Supplementary figure S5). The predominant respiratory quinones of strain 17J68-5^T were found to be MK-6 (33.7%) and MK-7 (66.2%). The results of these chemotaxonomic characteristics are consistent with those of most species in the genus *Hymenobacter* (Hirsch et al. 1999).

In conclusion, the results of 16S rRNA gene sequence analysis, the presence of PE, two unidentified aminophospholipids and a phospholipid as major polar lipids, MK-7 as the major quinone and the fatty acid profile showed that the strain 17J68-5^T is a member of the genus *Hymenobacter*. However, the differences such as the additional respiratory quinone and in the fatty acids (C_{12:0}, C_{15:1} ω6c, C_{17:1} ω6c, summed feature 1 and summed feature 3), together with ANI and dDDH values (< 95–96%; < 70%), indicated that strain 17J68-5^T can be distinguished from closely related *Hymenobacter* spp. Therefore, it is concluded that strain 17J68-5^T represents a novel species of the genus *Hymenobacter*, for which the name *Hymenobacter jejuensis* sp. nov. is proposed.

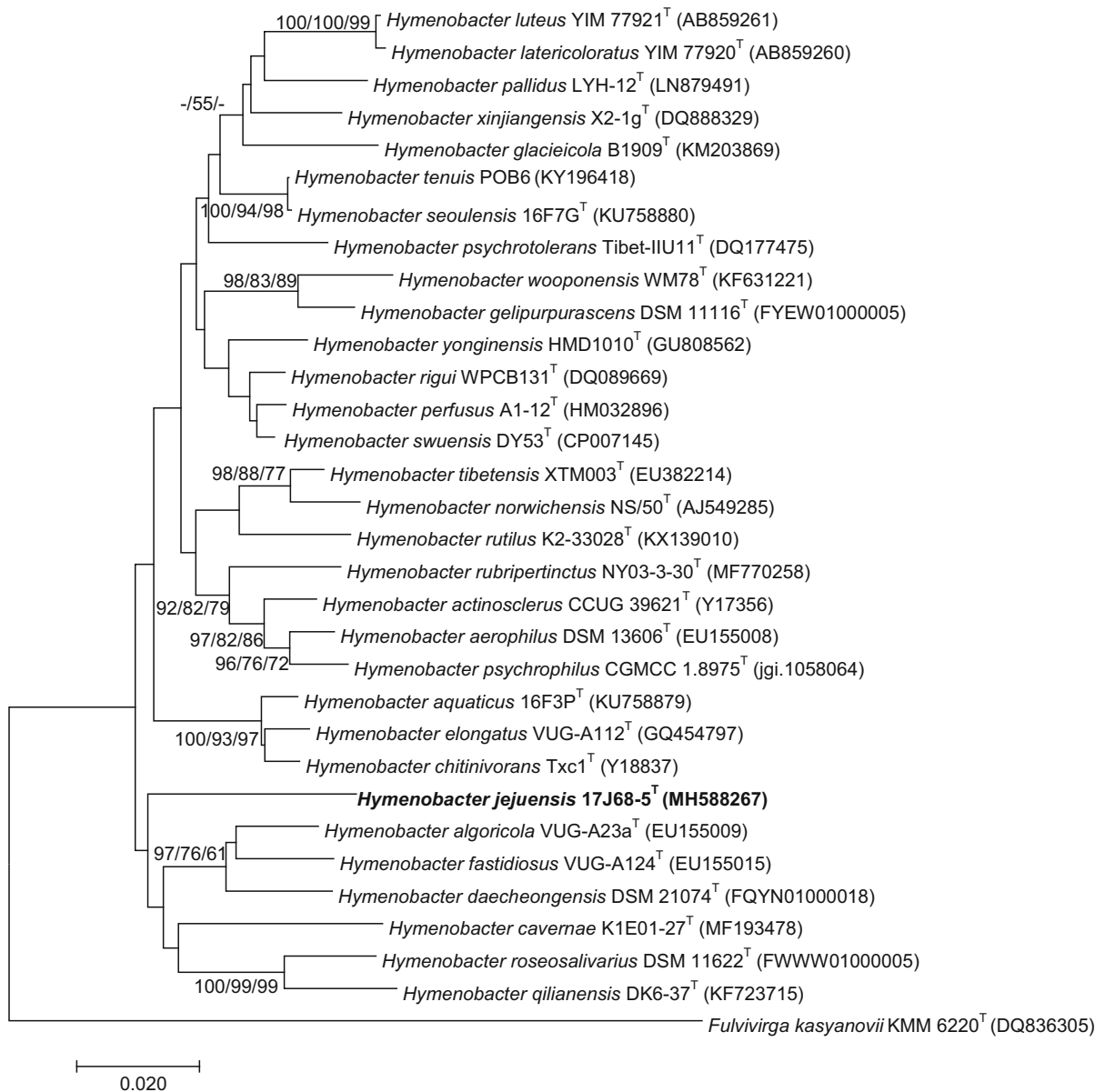


Fig. 1 Phylogenetic analysis of strain 17J68-5^T (in bold type) with closely related members of the genus *Hymenobacter* based on 16S rRNA gene sequences available from NCBI database (published). The tree was constructed using neighbor joining method and the same topologies was recovered from the

maximum-likelihood and maximum-parsimony algorithms respectively. Bootstrap values (> 50%) based on 1000 replications are shown at the branch nodes. Bar, 0.01 substitutions per nucleotide position. *Fulvivirga kasyanovii* KMM 6220^T (DQ836305) is used as an outgroup

The Digital Protologue database (Rosselló-Móra et al. 2017) TaxoNumber of strain 17J68-5^T is TA00996.

UV radiation resistance

In the UV radiation survival test, strain 17J68-5^T showed resistance to UV radiation (Fig. 2). Strain 17J68-5^T was tolerant of UV irradiation, showing a survival rate of 10% after exposure to UV light at a

Table 2 Cellular fatty acid profiles of strain 17J68-5^T and closely related species

Fatty acids	1	2	3	4
Saturated				
C _{12:0}	3.6	–	–	–
C _{14:0} iso	–	1.4	–	–
C _{15:0}	–	1.2	–	–
C _{15:0} iso	19.1	23.9	20.7	25.1
C _{15:0} anteiso	3.9	5.9	7.6	8.1
C _{15:0} iso 3OH	2.4	2.6	2.3	2.5
C _{16:0}	1.2	2.1	4.3	6.2
C _{16:0} iso	2.0	9.2	3.6	Tr
C _{17:0} iso	1.4	2.9	Tr	3.4
C _{17:0} iso 3OH	4.3	3.4	3.3	5.9
Unsaturated				
C _{15:1} ω6c	1.3	–	1.4	–
C _{16:1} iso H	3.1	8.5	4.3	–
C _{16:1} ω5c	13.1	16.9	10.6	14.1
C _{17:1} ω6c	1.9	–	1.3	–
Summed Feature 1 (C _{15:1} iso H/C _{13:0} –3OH)	2.4	–	1.3	Tr
Summed Feature 2 (C _{16:1} iso I/C _{14:0} –3OH)	–	1.9	–	–
Summed Feature 3 (C _{16:1} ω6c/C _{16:1} ω7c)	21.2	–	15.3	14.8
Summed Feature 4 (C _{17:1} iso I/C _{17:1} anteiso B)	17.9	6.8	8.9	7.5
Summed Feature 6 (C _{18:0} ante/C _{18:2} ω6, 9c)	–	10.8	–	–

Strains: 1, 17J68-5^T; 2, *Hymenobacter daecheongensis* KCTC 22258^T; 3, *H. rutilus* K2-33028^T; 4, *H. tibetensis* XTM003^T. Data for reference strains (except *H. daecheongensis*, this study) are from Kim et al. (2017) and Dai et al. (2009). Values are percentages of total fatty acids; fatty acids amounting to < 1% of the total fatty acids in all strains listed are omitted; Tr, Trace (< 1%); –, not detected

dose of 300 J/m². At this dose, *D. radiodurans* (DSM 20539^T), exhibited a 98% survival rate and *Escherichia coli* K12 exhibited a 0% survival rate, respectively.

Description of *Hymenobacter jejuensis* sp. nov

Hymenobacter jejuensis (je.ju.en'sis. N.L. fem. adj. *jejuensis* pertaining to Jeju Island in the Republic of Korea, from where the type strain was isolated).

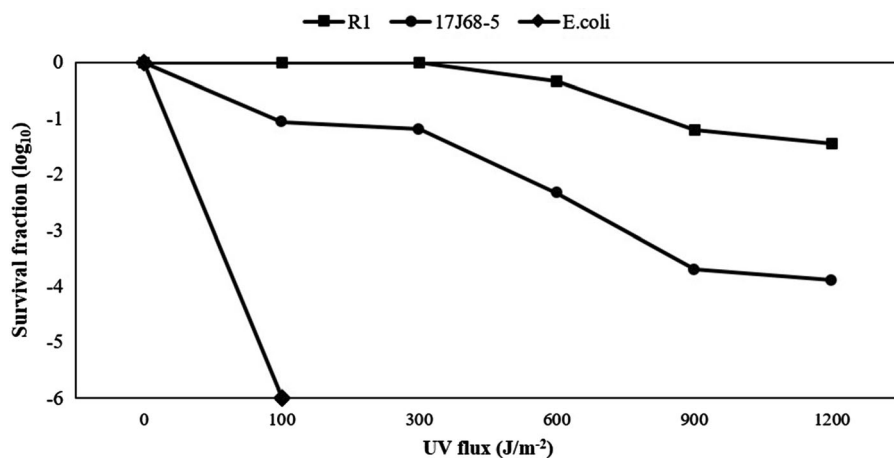


Fig. 2 Representative survival plot for strain 17J68-5^T (filled circle) following exposure to UV radiation. Survival rates of *D. radiodurans* R1^T (filled square) and *E. coli* K12 (filled diamond) are also shown. The survival rate after UV radiation was

measured using early stationary phase (~ 10⁹ CFU/ml) cells on R2A agar. Each increment on the y-axis represents a tenfold reduction in viability

Cells are Gram-stain negative, non-motile and rod-shaped. Colonies on R2A agar are convex, smooth, circular, pink-coloured and 4 mm in diameter after 3 days of growth at 25 °C. Cells are approximately 0.6–0.8 µm wide and 0.8–1.2 µm long. Growth occurs at 18–37 °C (optimum 25 °C) and at pH 6.0–7.5 (optimum 6.5). Cells do not show NaCl tolerance. Grows well on R2A agar and nutrient agar, but not on TSA and MacConkey agar. Catalase and oxidase activities are positive. The major polar lipid is phosphatidylethanolamine. The predominant respiratory quinones are menaquinone 6 and 7. The main cellular fatty acids are C_{15:0} iso, C_{16:1} ω5c, summed feature 3 (C_{16:1} ω6c/C_{16:1} ω7c) and summed feature 4 (C_{17:1} iso I/C_{17:1} anteiso B). The genomic G + C mol % derived from the draft genome of the type strain is 59.6.

The type strain, 17J68-5^T (= KCTC 62224^T = JCM 33182^T), was isolated from soil in South Korea. The GenBank accession number for the 16S rRNA gene sequence of strain 17J68-5^T is MH588267. The draft genome sequence of strain 17J68-5^T has been deposited in GenBank/DDBJ/EMBL under the accession number CP040896.

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Author's contributions All authors equally contributed in this work.

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Compliance with ethical standards

Conflict of interest All authors certify that there is no conflict of interest.

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